

Plant–Herbivore Interactions

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Interaction of herbivores with the landscape and the vegetation it supports may benefit both the landscape vegetation and the herbivore, but at other times the interaction may have adverse effects. Usually the herbivore is parasitic to herbaceous vegetation in the landscape, but herbivores aid in nutrient recycling and often the transfer of nutrients within the ecosystem, as well (Fig. 8.1). The interaction is characterized by constant change. For example, with each movement or biting activity of the herbivore the landscape changes, at least at the micro-scale. If availability of herbage is near the threshold for adequate support of herbivore demand, then each perturbation may constitute a diminished ability to fully support the animal's needs.

Landscapes in agricultural settings range from very extensive, as in the arid West of the United States, the outback of Australia, or steppes of Russia and China, to highly intensive and specialized monocultures (or at most binary mixtures) of the humid zones in Europe, New Zealand, and the eastern United States. The vegetative diversity within the landscape and the rate at which changes occur due to herbivore interactions are related to the degree of intensification. Due to the diversity and complexity of the grazed landscape, experimentation to determine causes and effects has been difficult and often misleading. Ecological assessment of species abundance and description often lacks the quantification required for making decisions and for economic evaluation by land managers. Mechanistic models could assist, but mathematical description of the interaction of herbivores with the grazed ecosystem has been difficult.

Management alters the interaction of domestic herbivores with the landscape and is addressed in other chapters (e.g., Chap. 43). This chapter will concentrate on

the interaction per se, given the resources and constraints within the defined landscape. The objectives are to characterize the dynamics that occur in the grazed landscape and the reaction of plants and herbivores to those dynamics.

Description of the Plant–Herbivore Interface

Landscape Attributes

The landscape is divided in a hierarchical manner into plant communities, patches, feeding stations, and plants (Fig. 8.2). Plant communities (large patches) are clustered in conjunction with geomorphic features (Senft et al., 1987), and these communities may be as simple as mono-specific sown pastures or as diverse as a species-rich rangeland. Diversity occurs in species of flora and fauna, spatial density in both vertical and horizontal planes, and in density of grazable herbage.

Within a plant community, small patches or feeding stations may be defined as areas grazed without the animal taking another step. The animal may choose a feeding station, then initiate a search among species, plants, and plant parts within the station to satisfy its nutritional needs. Plants within the feeding station constitute the available forage from which the animal may select, and the density of green leaf material within the canopy of plants influences the rate at which the animal harvests forage.

At the feeding station, contamination due to feces and urine, insect damage to the plant parts, and soil mounds due to mammals and insects may influence the desirability or the accessibility of forage on offer. As such, these biotic factors interact with the landscape, affecting the presentation of the diverse herbage from which the grazing ruminant must obtain its daily nutrient requirements.

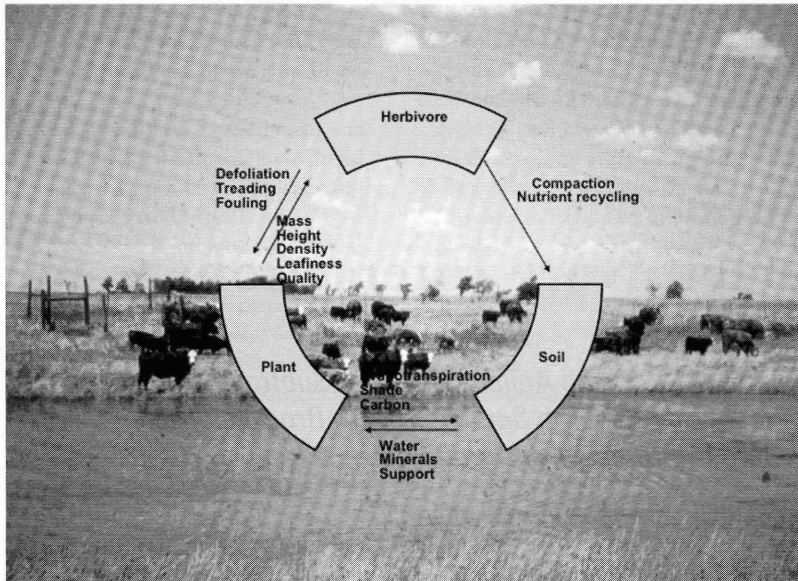


FIG. 8.1. Soil-plant-animal ecosystem and the primary interactions that occur among the major components.

Herbivore Response to Landscape Attributes

Grazing was defined by Arnold (1964) as “movement in a horizontal plane and selection in a vertical plane” but later was modified by Milne et al. (1979) into a two-phase concept involving site selection and biting activity. Herbivores eat to satisfy a need and a desire for nutrients, the most prominent being energy and protein (Coleman and Moore, 2003). The maximum level of intake occurs under ideal conditions, and when the nutritional needs are met, anatomical sensors send a signal to the brain that satiety has occurred (Chap. 32).

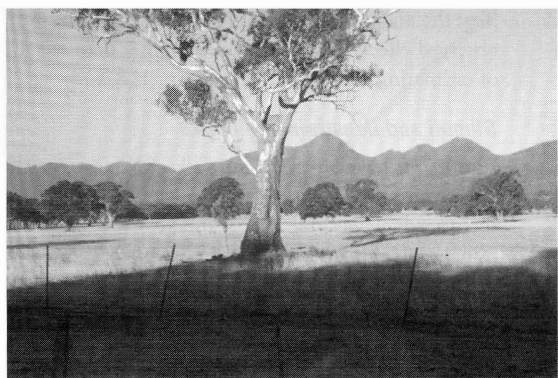
In many situations satiety does not occur because the animal is unable to satisfy its nutrient needs because the forage on offer lacks either sufficient quantity, quality, or both. The major impact of inadequate nutrition of grazing animals, whether the herbage is deficient in either quality (Weston, 1996) or quantity (Stobbs, 1973a, 1973b), is reduced dry matter (DM) intake (Hodgson, 1982a). If the forage on offer is low in quality, limits to intake due to deficient quantity are further exacerbated because it is the intake of digestible DM that determines performance, that is, the rate of gain (Coleman et al., 1999).

Animal Drives

Different drives influence herbivore movement within a landscape, and those drives have been ranked for domestic livestock in the following order: (1) thirst; (2) ambient

temperature as it influences homeothermy; (3) energy balance or hunger, the drive that most influences whether to graze or not; (4) time of day, for example, nighttime as it influences orientation and predator avoidance; and (5) rumination, rest, social facilitation, and sleep (Stafford-Smith, 1988). Drives with the momentarily higher priority, for example, the need for water or mitigation of heat extremes, may override the drive to graze. Hence, the intake drive for herbivores is the net result of physiological nutrient demand modified by the degree of satisfaction of higher-ordered needs. The intake demand is also modified by the residues and metabolic end products from the most recent meal. Herbivores must, at a given time, first choose whether to eat and then choose at which site or community to eat, which species, and for some animals, which plant part. Grazing strategy of herbivores has been studied and reported in detail (Malacheck et al., 1986; Arnold, 1987; Stuth et al., 1987; Provenza and Balph, 1988; and Chap. 44 in this volume).

In a monoculture, the grazing animal will likely seek areas that have been grazed recently because they contain new regrowth that is of higher quality than ungrazed material. However, if grazed too recently, low amounts of biomass may reduce rate of food intake. Forbes and Coleman (1993) observed that cattle (*Bos* spp.) grazing pastures with high average herbage mass and with substantial spot grazing had lower bite weight and total intake than did animals grazing pastures with less herbage

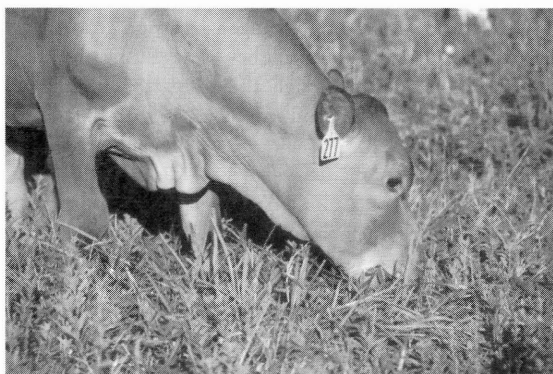


Landscape



Community or
Large Patch

Individual
feeding station



Plant



FIG. 8.2. The ecological hierarchy of the grazing system as encountered by large herbivores.

mass but that had been more uniformly grazed. As herbage height and available herbage becomes more restricted, the animal may enlarge the grazed area by grazing from the boundaries.

In a diverse landscape that includes not only grasses, but also forbs, shrubs, and trees, the choice of grazing station may be more complex, as suggested by the generalized diet-decision model for grazing herbivores (Stuth et al., 1987). The authors found that the probability of an individual tiller being grazed among tall grass prairies in Texas depended on forage species, previous defoliation, and number of live leaves. For instance, steers selected brownseed paspalum when its tillers were taller, but if tiller heights were equal they selected little bluestem, based on its relative abundance. Animals frequently revisited previously defoliated areas, and live leaf was always preferred over other plant parts. However, the factors changed with season and with stocking rate or grazing intensity. Stuth et al. concluded that our understanding of the complexities of diet selection was not sufficient to fully understand the plant–animal interface.

Components of Intake

Daily intake is a function of rate of intake and time spent grazing. Typically, and especially under stall-fed conditions, intake is measured over a long period of time (weeks) to eliminate day-to-day variation. However, determining how sward characteristics of pasture or range affect intake and diet quality under grazing is difficult because the sward is continually changing through the processes of growth, harvest, treading, fouling, and senescence.

The effects of canopy characteristics on intake have been investigated as short-term (< 30 min) components in a deterministic manner (Arnold, 1964; Stobbs, 1973b; Hodgson, 1982b). These authors theorized that

$$\text{Intake} = \text{intake rate} * \text{grazing time}$$

$$\text{Intake rate} = \text{intake per bite} * \text{rate of biting}$$

Thus

$$\text{Intake (24 h)} = \text{intake per bite} * \text{rate of biting} * \text{grazing time}$$

Variations in sward characteristics or canopy structure directly affect intake per bite and rate of biting. Variations in grazing time and, possibly, rate of biting, could be considered compensatory responses by the animal (Hodgson, 1982a; note trends in Fig. 8.3). Though somewhat mechanistic, this view of ingestive behavior and its impact on intake is useful for elucidating how behavioral responses to variation in sward characteristics may influence herbage intake. Since each of the components is impossible to measure without error, and some have inherent

bias, the methods are probably more useful for explaining observed effects on herbage intake rather than as a means of estimating intake itself (Hodgson, 1982b).

Stimuli and Constraints to Intake

Ruminants have an enormous task of harvesting enough fresh feed ($\sim 100\text{--}400 \text{ g kg}^{-1}$ live weight) daily to meet their needs. Digestible energy intake, the primary determinant of performance, is a function of both rate of intake and digestibility of the consumed diet and varies due to nutritional heterogeneity of the sward, seasonal production, and variation in the canopy structure (Chacon and Stobbs, 1976). Often, those plant characteristics that allow maximization of intake (e.g., high biomass) are antagonistic to others (e.g., high leaf density) that facilitate high diet digestibility. The process of selective grazing facilitates the grazers' attempt to optimize intake of digestible energy over a wide variation of sward conditions.

Area Density Constraints

Spatial distribution of leaf within the sward or canopy influences the ease with which animals satisfy their nutritional needs. With dense, leafy, temperate pastures, herbivores consume forage in large bites and can satisfy their appetite rather easily in grazing times of 6–8 h d⁻¹. Harvest rate is slower for cattle grazing certain warm-season grasses, even when large quantities of herbage are available, due in part to lower density of green leaf in the grazed horizon (Stobbs, 1974; Forbes and Coleman, 1993). In addition, longer rumination time between grazing periods may be required for warm-season forage diets. With slower harvest rates, grazing time on warm-season grasses may be further restricted to the point that digestible energy intake is less than that needed for optimum production.

Plant Constraints

The constraints to maximum (optimum) rate of intake differ among landscapes and the level of intensification (either intensively grazed improved pastures or extensively grazed rangelands). Intake rate by animals grazing planted pastures are more likely to be constrained by short herbage height or low vertical density of grazable material that limits optimum (maximum) bite weight (Jamieson and Hodgson, 1979b). In contrast, those grazing rangelands are more likely to be constrained by lower horizontal density such that the need to search may limit biting rate (Senft et al., 1987). Selectivity is likely to be greater under extensive conditions, and diet quality may be higher than in higher-density pasture.

Large bites of high quality forage are rare in most grazing environments, and as a consequence, the grazing animal is faced with a trade-off between bite weight and forage quality (Demment and Greenwood, 1988). More

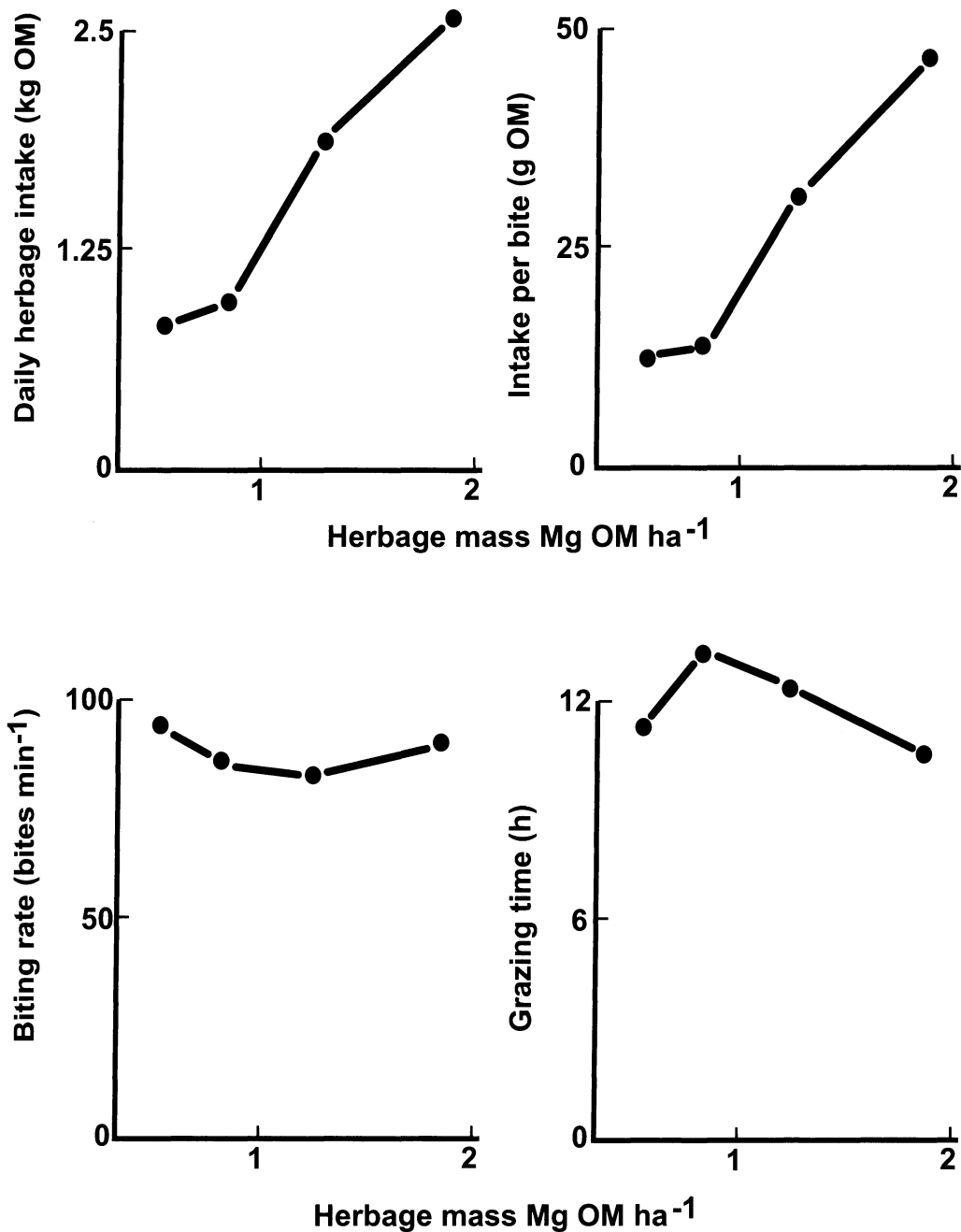


FIG. 8.3. The responses of herbage intake (*top left*), bite weight (*top right*), biting rate (*bottom left*), and grazing time per day (*bottom right*) to increased herbage mass of perennial ryegrass. (From Hodgson, 1982b; used by permission from the British Grassland Society.)

time may be spent pursuing more nutritious feed under extensive conditions, thus total intake may be diminished. Under more intensive conditions, forage height and mass are more consistent across the landscape, but at any one time quality may range from high to low. Swards differing in height or distribution through vertical space may limit bite weight and instantaneous intake rate. As this constraint becomes more severe, limits to compensation through biting rate and grazing time cause intake to be reduced (see Fig. 8.3).

Environmental Constraints

Environmental conditions influence grazing time and may be the most important non-canopy factor affecting grazing behavior (Hancock, 1950). For example, during summer in Florida, grazing time of lactating Holstein cows decreased linearly with increasing average solar radiation and temperature (Macon, 1999). Grazing time at night increased linearly as solar radiation during the day increased but not enough to compensate for the loss in grazing time during the day. Taken together, summer daytime temperature and solar radiation explained 83% of the variation in grazing time during the day, 95% of the variation at night, and 99% of the variation in time spent under shade during the day. To further complicate the matter, some animals within a species (e.g., *Bos taurus*) have different abilities to cope with nutritional or climatic constraints (Butts et al., 1971). Across animal species, adaptive mechanisms to high temperatures include smaller body size, higher surface-to-mass ratio, and more efficient prehensile apparatus.

Selectivity

Senft et al. (1987) suggested that selection by large herbivores is based on solving two opposing problems: obtaining maximal quality and adequate quantity. This strategy is influenced by herbivore characteristics that affect energy needs and by plant diversity within the landscape. Upon initiation of a grazing period, the first decision an animal must make is where to graze. In sown pastures, the choice may be quite limited, because there is only one plant community. However, patch grazing, dung fouling, location of water and feed (mineral) stations, and shade may affect the patch choice. In extensive rangelands and savannahs, spatial selection of plant communities and patches by the animal is influenced by the features of the landscape that affect animal movement patterns (Senft et al., 1987), including landscape boundaries, distribution of plant communities, and accessibility and distribution of water, shade, and bedding sites. In familiar environments, preferences for feed resources may result from previous experience with sensory, nutritional, and physiological consequences of sampling particular dietary items (Provenza and Balph, 1988). Sources of learning include food imprinting, social learning, and individual learning (see Chap. 44).

Dynamics at the Plant–Herbivore Interface

The plant–animal interface is the dynamic interchange between the herbivore and the ecosystem. Changes in the sward take place with each step, bite, and waste elimination by herbivores. These changes affect instantaneous growth rate of affected plants and herbage available for the next bite by the herbivore. Sward changes caused by the herbivore tend to be more drastic than those associated with the more gradual changes that occur during growth of different plant tissues. As the herbivore continues to move and graze, other plants are affected, grazing stations are altered, and the herbivore must move to another grazing station (as in Fig. 8.2) or maintain its current grazing station and have its diet be affected by grazing-induced alteration of the vegetation.

The sward canopy may be characterized by proportions of relative amounts of new growth and senesced material (Fig. 8.4); of leaf, stem, and inflorescence; of plant species; or of combinations of the above. Determinations of the separate components are laborious and, hence, are seldom attempted in research; only the standing biomass is measured. Due to the interactions of the herbivore with the plant canopy, the dynamics of plant growth rate and harvest rate generally cannot be described by empirical relationships. Rather, mechanistic models that integrate the individual components over time provide a more realistic approach (Bircham and Hodgson, 1983; Lantinga, 1985; Smith, 1985). Leaf area of a sward affects solar radiation interception and shoot mass accumulation rate of forage plants. Growth rate also tends to increase with increasing sward DM mass and height (Bircham and Hodgson, 1983). Conceptualizing growth rate as a function of herbage biomass fits well with the concept that bite weight and intake rate by herbivores are also primarily a function of herbage or leaf biomass. Hence, both growth rate and harvest rate can be modeled in the same terms, attributes, and units.

Sward Canopy Effects on Animal Response

Canopy Factors Affecting Choice of Feeding Stations

The interaction of herbivore behavior with the landscape can be separated into a hierarchy of spatial and temporal scales (Laca and Fehmi, 1999). Laca and Fehmi hypothesized that grazing animals sense and process information about their environment and internal state at multiple hierarchies or scales (e.g., Fig. 8.2) simultaneously and then choose the type and scale of behavior based on the information and previous experience. A simple example is that if intake rate or bite weight within a patch declines below a certain threshold, animals may choose to ignore smaller feeding stations within the patch and move to another patch. Animals exert greater selectivity among units at larger scales, presumably because larger

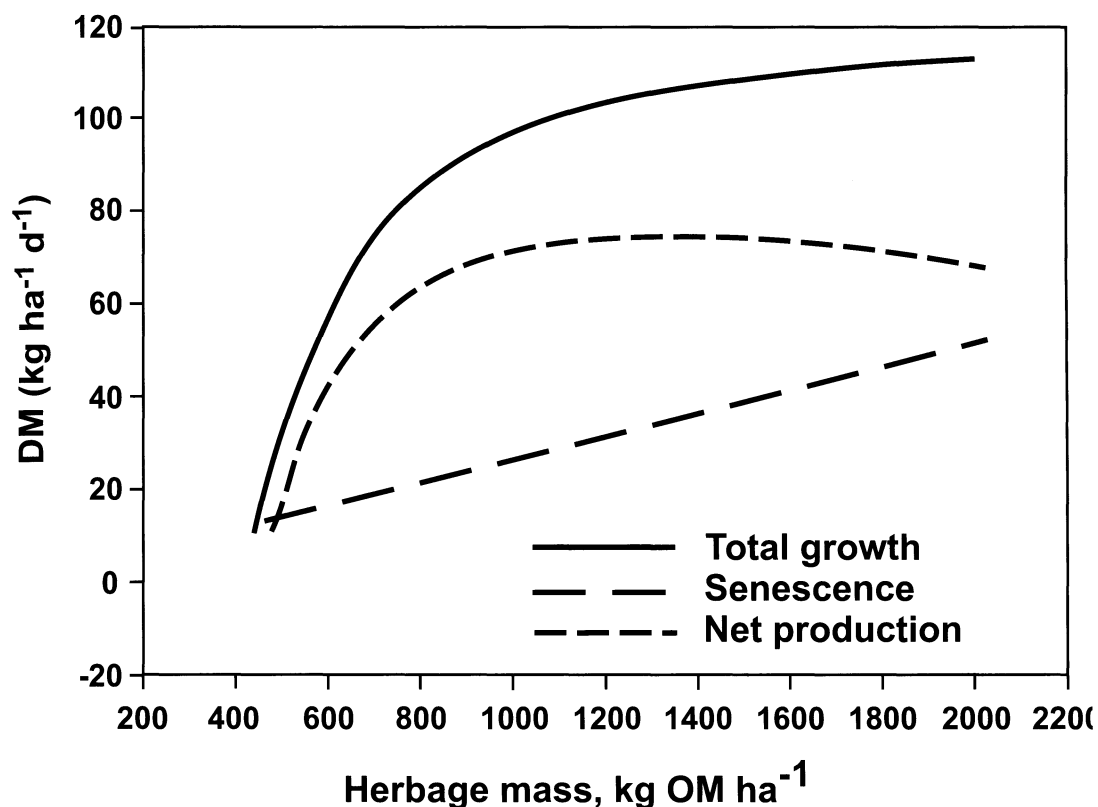


FIG. 8.4. Components of a ryegrass sward. The relationship between rate of total growth, rate of senescence, and net production rate of green herbage to herbage mass. (After Bircham and Hodgson, 1983; used by permission from the British Grassland Society.)

scales are easier to remember and because of the time and energy demands of locomotion (Laca and Fehmi, 1999). Selectivity is also more pronounced in large than in small patches (Wallis DeVries and Laca, 1997). However, the number of bites per feeding station is not influenced by patch size, suggesting that selection between feeding stations is a different process than selection within a feeding station. It also appears that animals do not treat larger patches as discrete feeding stations, but rather as a continuous resource.

Canopy Factors Affecting Selection Within a Feeding Station

Animals select for leaf and live herbage and discriminate against dead material; as a result, the nutritive value of the herbage consumed is greater than that of the available herbage mass (Fisher et al., 1991). Low bulk density in the upper layer of an aescynomene–limpograss canopy allowed for selection of legume early in a grazing period. As grazing continued, legume leaf mass became

limiting and herbage bulk density increased, effectively ending selection for the legume (Sollenberger et al., 1987). When dallisgrass (Flores et al., 1993) micro-canopies were short and dense, stems presented a barrier that made it difficult for the animal to insert its muzzle and select leaves below the height at which stems occurred in the canopy. This effect was negligible when stems were taller and sparse because cattle pushed them aside to access leaf.

Many plants that have evolved under grazing have developed either chemical or physical deterrents to grazing (Dougherty, 1989). Antiquality components such as tannin, lignin, or alkaloids discourage animals from grazing too intensively either through metabolic feedback or taste (Malachuk et al., 1986). The occurrence of secondary plant metabolites is clearly related to rejection by herbivores (Illius and Hodgson, 1996). In *Brachiaria* spp.–*Desmodium* spp. pastures, selection against the legume was attributed to its high tannin concentration (Lascano, 1999).

Table 8.1. Ranges in bite weight of cattle measured as weight of esophageal extrusa reported for various types of forages

Forage Type	Animal Class	Bite Weight, mg OM Bite ⁻¹ kg BW ⁻¹	Reference
Tropical grass	Cows	0.47–0.98	Stobbs, 1973a
Tropical grass	Cows	0.18–0.83	Chacon and Stobbs, 1976
Old world bluestem	Steers	0.45–1.42	Forbes and Coleman, 1993
Limpograss/ <i>Aeschynomene</i>	Steers	1.13–5.77	Moore et al., 1987
<i>Lablab purpureus</i>	Cows	0.24–1.09	Hendricksen and Minson, 1980
Ryegrass	Calves	0.31–4.09	Jamieson and Hodgson, 1979a
Ryegrass	Cows	0.59–1.43	Forbes and Hodgson, 1985
Ryegrass	Cows	1.25–3.24	Hodgson and Jamieson, 1981
Ryegrass	Calves	1.48–2.46	Hodgson and Jamieson, 1981

Canopy Factors Affecting Intake and Performance

Forage intake of stall-fed animals is governed largely by the capacity of the rumen and the rate at which the ruminal contents are digested or removed by passage (Weston, 1996; see also Chap. 32). Intake of dense pasture forages is normally governed by the same mechanism. An exception occurs when digested nutrients initiate satiety in the brain before the rumen is filled by animals grazing high-quality immature growth or cereal forage. In these cases, animals graze each day in eight or more short periods of 1–2 h rather than the normal 3- to 4-h-long periods (Coleman and Phillips, 1991). In addition to distension of the rumen or satiety (see Chap. 32), intake of grazing animals may be constrained by factors such as herbage being too short (Hodgson, 1982a) or leaf density being too low in the grazed horizon (Stobbs, 1973b).

A considerable body of evidence has shown that bite weight is more important than biting rate or grazing time in the control of total daily intake (Fig. 8.3) (Stobbs, 1973a; Hodgson, 1982a; Forbes and Coleman, 1993). Bite weight can be measured directly using animals fistulated at the esophagus or indirectly from measured daily intake divided by total daily bites (Hodgson, 1982b). Both methods have potential for errors and large inherent variation. Published estimates of bite weight vary considerably depending on the type of forage, stage of growth, relative abundance, and class of herbivore (Table 8.1 and Forbes, 1988). In general the maximum bite weight of cattle grazing temperate forages was larger than that of cattle grazing tropical swards, but minimums were similar across forage types, likely due to the constraint of herbage mass.

Quantity of Herbage Available

Bite weight and herbage intake increase linearly with sward surface height and herbage mass in both temperate

(Allden and Whittaker, 1970; Hodgson, 1981) and tropical (Chacon and Stobbs, 1976) pastures, but slopes of the increase were different among forage species (Forbes, 1988); therefore, no unifying relationship could be established from these published reports. The relationship of sward height or mass with intake rate and animal performance is inconsistent among C₄ grasses. Across a wide range of stocking rates of rotationally stocked stargrass pastures, daily gain of cattle increased with increasing herbage mass (Hernández Garay et al., 2004). In contrast, when limpograss pastures were continuously stocked at a density to maintain 20-, 40-, and 60-cm sward heights, herbage mass increased linearly with increasing height, but daily gain of yearling cattle increased with canopy height only up to 40 cm (Newman et al., 2002). Lower gains at 60 cm were due to greater lodging and trampling of this forage and lesser accessibility of leaf, suggesting that increasing mass and height are not always sufficient to guarantee greater gains and that other canopy factors may be more important in some situations. In highly heterogeneous rangelands, no simple relationships between intake or performance and herbage mass or sward height have been found (Gordon and Lascano, 1993).

Black and Kinney (1984) found that intake rate of sheep (*Ovis aries*) grazing herbage from hand-constructed wimmera ryegrass swards was related to sward height only when tiller density did not vary and to sward bulk density only when sward height was constant. They found that intake rate was more closely related to herbage mass, but the relationship was asymptotic, with the maximum intake achieved at a herbage mass of about 1000 kg ha⁻¹. Similarly, Forbes and Coleman (1993) found that intake rate of cattle grazing old world bluestem herbage peaked at 1070 kg ha⁻¹ of green herbage mass. Because the ryegrass swards were mostly green herbage, the expression of mass as green or green leaf may help to unify the relationships across species. Penning (1985) also presented

evidence that intake rate of sheep grazing perennial ryegrass reached an upper limit when sward height exceeded 70 mm.

In general, as sward height and the resultant bite weight decreases, animals may compensate by increasing grazing time and, to a lesser extent, biting rate (see Fig. 8.3). However, both are limited in the range of compensation to about 15% of that at optimum bite weight (Forbes, 1988). Increased grazing time as a response to decreased bite weight is constrained by other drives such as the need to socialize, ruminate, and rest, whereas increased biting rate may be constrained by sward structure because the animal spends more time searching within the grazing station for desired plant parts.

Herbage Quality and Presentation of Nutrients

The source of available herbage can be generally characterized as green leaf or stem, dead leaf or stem, and inflorescence. The source of species are generally grasses, legumes, other forbs, and shrubs. The quality of the various plant tissues tends to follow the following order: legume leaf > forb leaf > grass leaf > legume stem > grass stem > shrub leaf > forb stem > shrub stem. However, exceptions do occur.

The sward canopy is defined as the aboveground parts of a sward and includes consideration of distribution and arrangement of plant parts. Attributes of the sward canopy, other than mass or height, that affect harvesting by animals include canopy density, species and plant part proportion, spatial arrangement of species and plant parts within the canopy, and chemical composition of selected parts (Stobbs, 1973b; Stuth et al., 1987; Coleman et al., 1989; Gordon and Lascano, 1993; Sollenberger and Burns, 2001).

Leaf bulk density of C_4 grass canopies is often lower than that of temperate grasses (Sollenberger and Burns, 2001), which is suggested as one reason for the lesser performance of livestock grazing C_4 compared with C_3 grass pastures (Stobbs, 1973a, 1973b). However, the relationship between leaf bulk density and animal response can be highly negative or positive depending on the spatial arrangement of leaf relative to stem (Sollenberger and Burns, 2001); thus, even swards with high leaf bulk density may not produce high animal gains. Green herbage mass or green leaf proportion in the canopy and, more specifically, in the grazed horizon, show a much more consistent positive relationship with bite weight, particularly in C_4 grass pastures (Burns and Sollenberger, 2002).

Several studies have shown that not only presence but also spatial arrangement and accessibility of leaf are important. For example, switchgrass pastures had a lower percentage of leaf (29% vs. 37%) and higher percentage of stem (54% vs. 47%) than did bermudagrass (Burns et al., 1991; Fisher et al., 1991). Leaves grew higher than stems in the switchgrass canopy, however, making it pos-

sible to select for leaf and produce greater daily gain for cattle (0.59 kg) compared with bermudagrass pastures (0.22 kg). Forbes (1988) concluded that in vegetative swards, bite weight increases as a result of the increase in sward height. When inflorescences were present at the top of the canopy, however, bite weight and intake rate were likely to be more closely related to sward density or leaf proportion.

Vertical heterogeneity in the distribution of nutrients occurs as a consequence of the spatial arrangement of different species and plant parts in grazed swards. Fisher et al. (1991) compared in vitro dry matter digestibility (IVDMD) by 5-cm vertical strata for three C_4 (bermudagrass, flaccidgrass, and switchgrass) and one C_3 grass species (tall fescue). All grasses were continuously stocked during the same time of year in North Carolina, and canopies were of comparable height when sampled. They found that from the bottom to the top layer, IVDMD increased by 21 g kg⁻¹ for tall fescue, 31 g kg⁻¹ for bermudagrass, 58 g kg⁻¹ for flaccidgrass, and 68 g kg⁻¹ for switchgrass. Leaves predominated in the tall fescue canopy, while stem and dead material were more prominent throughout the C_4 grass canopies. Limpograss canopies were 33% leaf in the top half compared with 10% leaf in the bottom half (Holderbaum et al., 1992), resulting in herbage crude protein in the top half being twice as great as that in the bottom half. In general, C_4 grass canopies possess greater vertical heterogeneity in terms of plant-part proportion and nutritive value than C_3 grass canopies.

Animal Species and Properties

Animals initiate a grazing bout to satisfy total intake (appetite) needs. Herbivores may be divided into three major classes: concentrate selectors, intermediate feeders, and bulk and roughage eaters (Van Soest, 1994). Subgroups of concentrate selectors include fruit and foliage selectors or tree and shrub browsers. Typically, these are not agriculturally important animals. Intermediate feeders include goats (*Capra hircus*) and sheep and as a group may be subdivided into forb- and browse-preferring or grass-preferring herbivores. Bulk and roughage eaters include larger ruminants such as cattle and are subdivided into fresh-grass grazers, roughage-grazers, or dry-region grazers.

Accessibility of more nutritious herbage is more important to intermediate feeders than bulk eaters. As intermediate feeders, sheep and goats have mouthparts and tongues adapted for a high degree of selectivity. In studies on indigenous hill-plant communities in Scotland, sheep usually graze deeper within the sward canopy than cattle and select a diet containing higher proportions of live leaf and broad-leaved plants (Hodgson, 1982a).

Bite weight varies with the volume of sward the animal can enclose in each bite and with the bulk density of the grazed horizon (Illius, 1997). Illius and Gordon (1987)

predicted that the allometric exponent relating bite weight to the animal's body mass (Wt) changed from 0.72 to 0.36 as sward surface height was progressively reduced. Comparing bite weight with the animal's metabolic requirements, which scale with $Wt^{0.75}$, large animals would be predicted to be at a disadvantage compared with smaller ones when grazing short swards because each bite represents a smaller proportion of daily requirements.

Animal Effects on the Sward Canopy During Grazing

The herbage canopy, characterized by its vertical and horizontal density, is the predominant attribute influencing the rate of intake (Stobbs, 1973b). The proportions of leaf versus stem and inflorescence and of green versus dead also influence the need for selectivity and, thus, the rate at which the available forage can be harvested. However, as grazing proceeds by an animal or a herd, sward changes result from animal action such as defoliation, treading, and fouling by defecation or urination. Individual plants and plant types vary in tolerance to grazing and trampling due to short-term physiological and longer-term morphological responses to substantial tissue loss. The mechanisms that allow rapid recovery and thus tolerance of herbivory are covered in a review by Richards (1993).

Defoliation

In species-diverse landscapes, tissue removal, especially as affected by selective grazing, changes the competitive dynamics among the plant species and changes succession rates (Heitschmidt, 1993). As herbage diversity increases, the animal has more choices and may select a diet of higher quality. However, diversity often occurs in less-dense herbage canopies and thus bite weight may be limited. Under these circumstances, the trade-off between maximizing selectivity and maximizing bite weight is likely influenced by animal species and physiological state (growing, mature, lactating, pregnant), as well as the diversity and density of the sward.

Rate of growth for whole plant biomass generally fits a sigmoidal curve (Bryan et al., 2000), with an asymptotic maximum during reproductive growth stages (see Fig. 8.4). Leaf defoliation of immature plants interrupts this growth curve, and at the instant of defoliation, new processes and dynamics take place (Richards, 1993). Upon defoliation of photosynthetically active tissue, C gain is reduced and translocation of previously fixed C ceases. Substantial change in the C and N economy begins within hours after the defoliation event. Other adaptive processes include compensatory photosynthesis and phenotypic plasticity (Chap. 42). Compensatory photosynthesis is the ability of mature leaves to rejuvenate their photosynthetic capacity to that of younger leaves or of younger leaves to slow the normal decline in photosyn-

thetic capacity with aging. Phenotypic plasticity is a longer-term response to defoliation stress and refers to changes in size, structure, and spatial positioning of plant organs that result in increased grazing tolerance or avoidance (Huber et al., 1999).

Defoliation intensity directly reduces whole-plant photosynthesis or daily C gain, but not necessarily in direct proportion to leaf-area loss, because canopy microclimate changes after each defoliation bite. When a portion of the canopy is removed, light penetration and interception by the new canopy affects the photosynthetic contribution of different ages and classes of leaves, some of which may be more efficient than those in the old canopy. If mature, previously shaded, and photosynthetically challenged tissue predominates on the defoliated plant, then subsequent canopy photosynthesis is likely to be greatly reduced. However, if young tissue remains, then photosynthesis is more proportional to leaf area.

Treading

Hoof action may affect pasture plants directly by damaging, severing, or partially burying plant tissue. Indirect effects of treading are mediated through changes in soil characteristics that influence plant growth and persistence (Pott et al., 1983). Plants' ability to tolerate the direct effects of treading are related to growth habit and morphology. However, grazing management (e.g., rotation) may help overcome the vulnerabilities. Vine-forming species such as kudzu or siratro are very susceptible to treading damage. Plants with protected bud sites and greater tensile strength may be more tolerant. For example, digitgrass, a stoloniferous perennial, was more tolerant of treading by sheep across a range of stocking rates than the legume *Lotononis* (Pott et al., 1983). Grazing management may play a role. The legume *aeschynomene* showed fewer adverse effects of treading if grazed initially when it was 20–40 cm tall than if grazed when 60–80 cm tall (Sollenberger et al., 1987). At the taller heights, the stem was woody and brittle and much more susceptible to breakage when stepped on by cattle.

There are mediated, or indirect, effects of treading. Soil bulk density is increased by animal traffic, but soil texture determines the degree to which compaction occurs (Krenzer et al., 1989). For example, bulk density increased for fine-textured soils as grazing intensity increased, but there was no effect of grazing intensity on bulk density of coarse-textured soils. In a white clover–perennial ryegrass pasture growing on a silt-loam soil, surface-soil bulk density and penetrometer resistance were increased by the second year of grazing because of treading (Kelly, 1985). In this study, pasture defoliation was uniform across the treading and no-treading treatments; electric fence was placed in such a way that grazing without treading was achieved on the no-treading treatment. By the third and fourth years, these soil

changes were associated with 1.5 and 2.3 Mg ha⁻¹ decreases in pasture production.

Grazed winter wheat pastures in Oklahoma had greater soil bulk density and strength than did ungrazed swards, resulting in lower soil water concentration in grazed areas (Krenzer et al., 1989). This was attributed to a reduction in the number of larger soil pores and total pore space. Reduced water infiltration can also occur with greater grazing pressure because of a reduction in vegetation and litter, both of which help decrease the impact of raindrops and create a rougher microtopography that increases infiltration under optimal grazing pressure (Naeth et al., 1990).

Excretion

Excretion affects nutrient cycling, pasture growth, and animal grazing patterns. In meat and fiber animals, the percentage of ingested nutrients retained and exported in body tissue is quite low, and most mineral nutrients consumed are excreted in feces and urine. A single urination from mature cattle may provide the equivalent of 5 mm of rain and 400–500 kg N ha⁻¹ on the 0.4 m² of ground that it covers, while dung usually covers about 0.1 m² and supplies the equivalent of 110 kg P and 220 kg K ha⁻¹ (Haynes and Williams, 1993). Nutrients excreted in urine are either volatilized (NH₃), plant available, or mineralized in a few days, while the nutrients in dung generally become plant available more slowly (Mathews et al., 1996). The pattern of dung and urine distribution to the pasture is nonuniform, and the nutrients contained are subject to loss from the system in a variety of ways, contributing to pasture degradation in production systems with minimal fertilizer input (Sollenberger et al., 2002).

Those nutrients retained do stimulate plant growth. For example, urine patches in a little bluestem–kentucky bluegrass mixture contained 112 g m⁻² more aboveground biomass and 2.5 g m⁻² more plant N than unaffected areas (Day and Detling, 1990). After a relatively short time, animals do not discriminate against urine-affected areas provided the forage is grazed before it becomes too mature. Much to the contrary, in a Colorado study natural urine patches covered only 2% of the surface area, but they contributed 7%–14% of aboveground herbage consumed (Day and Detling, 1990). In contrast, dung initially causes rejection of surrounding herbage, such that plant maturity is the likely reason for islands of ungrazed herbage that continue to exist over time. However, in mixed-species (animal) grazing, animals different from the species depositing feces often preferentially graze herbage near dung pats.

Optimizing the Plant–Herbivore Interface

One genetic attribute of a plant species (or ecotype) might be described as the herbage mass that provides sufficient leaf area to support maximum growth rate under

optimum climatic conditions. If this assumption is true, then maintaining that herbage mass and leaf area by grazing management should optimize plant growth rate and harvest rate (Bryan et al., 2000). Overgrazing (too many herbivores for too long) would reduce herbage mass and leaf area below the level for maximum plant growth and thus reduce instantaneous growth rate and average growth for the next growth (rest) cycle. If the herbivore density or animal demand remains constant at the high level, the sward will continue to deteriorate at an increasing rate. Conversely, if harvest rate is less than the growth rate, plant biomass accumulates, plants mature, and forage quality declines. In this scenario animals concentrate future grazing bouts on previously grazed areas that are less mature, but that may not have had an adequate rest period, that is, patch grazing occurs. In this case, optimum defoliation rate over the landscape may not be achieved because overgrazing is imposed by the herbivore in the selected area.

Summary and Conclusions

Although considerable achievements have been made in understanding interactions that take place at the plant–herbivore interface, integration of the dynamic processes that instantaneously drive the various components remains unsolved. Accuracy of intake predictions for grazing animals will likely remain limited until a better understanding exists regarding how animals reconcile the costs and benefits of grazing activity and how to integrate grazing management with inherent herbage constraints to digestion and processing of undigested residues. That being said, much more progress has been made in ascertaining the short-term impacts of the sward on rate of intake and selectivity than has been made on determining the immediate response of plants to defoliation and other disturbances by grazing. Mechanistic models on plant growth and animal intake should be combined and integrated to evaluate our current understanding of the dynamics of the plant–animal interface in quantifiable form.

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